

THE GENERIC AND SUBFAMILIAL CLASSIFICATION OF THE NAIDIDAE (ANNELIDA: OLIGOCHAETA)

R. O. Brinkhurst

Abstract. — Examination of the characters used to define genera within the family Naididae leads inevitably to the conclusion that the genus *Pristina* Ehr. requires subdividing into two genera, *Pristina* and *Pristinella* n. gen. Neither classical nor quantitative methods support the division of the family into subfamilies, but the latter support the erection of the genus *Pristinella* n. gen.

During the preliminary stages of an assessment of alternative quantitative approaches to classification of the Oligochaeta all generic characters currently applied in the family Naididae were examined, as was the subfamilial classification. Both of these have been accepted uncritically since they were revised by Sperber (1948), who reviewed the historical basis for that classification. Four subfamilies were recognized. Two are monotypic (*Pristininae*-*Pristina* Ehr., *Paranaidinae*-*Paranais* Czern.), the third contains two genera (*Chaetogastrinae*-*Chaetogaster* von Baer, *Amphichaeta* Tauber), and the fourth, the *Naidinae*, contains all other genera and is therefore disproportionately large. While this is not of itself evidence for the unsuitability of the existing classification, it does suggest careful re-examination. An intensive effort to examine quantitative means of doing this is underway; this provisional report is required in order to allow other publications to proceed based on the division of the genus *Pristina* in particular.

Paranaidinae Sperber, 1948

Sperber (1948) established this subfamily based on the unique characteristic of absence of nephridia, even in budding segments. Additional characters cited were a reduction of the number of anterior segments formed on budding from 5 to 4, despite the fact that this is shared with *Stephensoniana* Cernosvitov, but the latter was held to be "otherwise so unlike *Paranais* that they can hardly be supposed to be especially related to each other." The male ducts are also said to be unusual, with narrow vasa deferentia, strongly muscular atria and no prostate glands, with other unusual characters in the ejaculatory ducts and clitellum. These are not, in fact, unique to the group (see the presence of the clitellum between the male pores in *Piguetiella* Sperber, for example) nor are the absence of both hair setae and eyes and the resemblance of dorsal and ventral needles. Since these studies, the genus *Wapsa* was defined, but a careful revision of North American species has shown that this is synonymous with *Paranais* (Brinkhurst and Coates 1984) and that both may possess nephridial tissue. Quantitative methods (see below) confirm the synonymy of these two genera and the lack of any clear separation of *Paranais* from all other genera, particularly *Chaetogaster*, *Amphichaeta*, and *Homochaeta* Bretscher.

The closed or even absent nephridia in many species of *Paranais*, *Amphichaeta*, and *Chaetogaster* may be associated with the estuarine habit of most species of

the first two. This explanation will not suffice for the latter, though, as this is predominantly a freshwater genus. It may be that *Chaetogaster* is derived from a common ancestor of all three genera.

There is no clear basis for the separation of the Paranaidinae, either by cluster analysis based on overall similarity or by virtue of shared advanced characters (synapomorphy).

Chaetogastrinae Sperber, 1948

This subfamily consists of two genera (*Chaetogaster* and *Amphichaeta*) that have a strongly lengthened pharynx, (which lacks the dorsal diverticulum of other genera but is connected to the body wall by strong muscle fibers), a short oesophagus, a stomach of unusual form, a strongly reduced vascular system and closed nephridia.

The nephridial characteristic is now known to be shared with *Paranais*, as described above. The possible functional reason for the reduction in the vascular system remains obscure, but the other characteristics, along with the reduced prostomium, are clearly associated with the adoption of a predatory mode of feeding. In most aquatic oligochaetes the roof of the pharynx is everted through the mouth in feeding, being returned by strong retractors. The glandular cells are greatly expanded by relocating the cell bodies on the septa of post-oral segments (the pharyngeal or septal glands). The pharyngeal diverticula of most naidid genera appear to be no more than large folds on either side and behind the pad-like pharyngeal roof which contacts the substrate once everted through the mouth (Sperber 1948, plate V fig. 5, plate VI fig. 1). The glandular cells of the pharynx are not often exported to form pharyngeal glands, and the retractor muscles may be poorly developed in the Naididae. The retractor muscles of the pharynx of the Chaetogastrinae are presumably developed from those present in other aquatic oligochaetes, but a comparative study of the pharyngeal structures would be in order to judge from the lack of recent descriptions of these structures.

There is no a priori reason to suppose that this pharyngeal modification was independently acquired by these two genera, but this is not in itself perhaps enough to provide the basis for a subfamilial classification. I would prefer to see independent characters that confirm a separation between these two genera and all other naidids. In fact, in most cluster analyses (see below), *Chaetogaster* is most closely aligned with *Homochaeta* Bretscher, which Sperber classified with the Naidinae, and only secondarily groups with *Amphichaeta* and *Paranais*. There is no clear evidence of a monophyletic group consisting solely of *Chaetogaster* and *Amphichaeta*.

Naidinae Lastockin, 1924

According to Sperber (1948), this subfamily was originally established to incorporate all genera bar *Pristina* (Pristininae Lastockin, 1924), but was modified by her to exclude the foregoing. Even then, Sperber admits that this subfamily is "more heterogeneous" than the others. There are no distinct characters that identify this group as a monophyletic assemblage by virtue of shared apomorphies, and they do not cluster out in a single group without the interposition of some or all of the genera excluded from the subfamily.

Pristininae Lastockin, 1924

The single genus in this subfamily is said to be "large and extremely varying, yet curiously homogeneous" by Sperber (1948). There follows a recitation of the subfamilial characters, which include a characteristic stomach with intracellular canals and male ducts which, while variable, have narrow atria without prostates with vasa deferentia entering at the top. The genital setae are of peculiar forms not seen elsewhere, according to Sperber.

The stomachal canals need to be re-investigated using electron microscopy.

The genus *Pristina* (as *Pristina* A and B) never appears separated from all other genera in any of the many analyses performed to date, though it is never consistently associated with any other genera. As none of the other subfamilies can be supported, there seems little point in returning to the position adopted by Lastockin, with this subfamily being contrasted to all others.

Even a superficial examination of the list of species currently included within *Pristina* suggests that it has been treated differently from all other genera. The presence or absence of a proboscis is used as a generic character throughout the rest of the family. Beginning with a breakdown based on that sole characteristic, it rapidly becomes clear that other, unrelated, characters are associated with this criterion, leading to the separation of two quite distinct genera as follows:

Pristina Ehrenberg, 1828

Type species.—*P. longiseta* Ehr.

Included species.—*synclites* Steph., *peruviana* Cern., *aequiseta* Bourne, *longiseta* Ehr., *proboscidea* Bedd., *breviseta* Bourne, *plumaseta* Turner, *leidy* Smith, *americana* Cern., *macrochaeta* Steph.

Definition.—Dorsal setae from II, hair setae present, ventral setae progressively differ from anterior to posterior bundles. Proboscis present. Septal glands present in some segments from III–VI. Stomach in VII or VIII with canals. Testes and spermathecae in VII, ovaries and atria in VIII, genital setae on VI, VI and VIII, or VII and VIII with glands. Prostates on the vasa deferentia. Spermathecae present. Cosmopolitan.

Pristinella, new genus

Type-species.—*Naidium bilobatum* Bretscher, 1903.

Included species.—*rosea* (Piguet), *amphibiotica* (Last.), *notopora* (Cern.), *jenkinae* (Steph.), *sima* (Marcus), *longidentata* (Harman), *menoni* (Aiyer), *idrensis* (Sperber), *acuminata* (Liang), *bilobata* (Bret.), *osborni* (Walton), *longisoma* (Harman), ? *arcaliae* (Pop.).

The genus is quite similar to the older assemblage associated with the name *Naidium* Schmidt but because *N. luteum* Schmidt, the type-species, is a tubificid, the generic name is not available (Sperber 1948:211).

Definition.—Dorsal setae from II, hair setae present, ventral setae progressively differ from anterior to posterior bundles. Proboscis absent. Septal glands in some segments from III–VI. Stomach in VI, VII or VIII, with canals. Testes and spermathecae in VII, ovaries and atria in VIII. Genital setae absent, or present in VIII in one species. Prostate glands absent. Male pores median in one species. Spermathecae absent. Cosmopolitan.

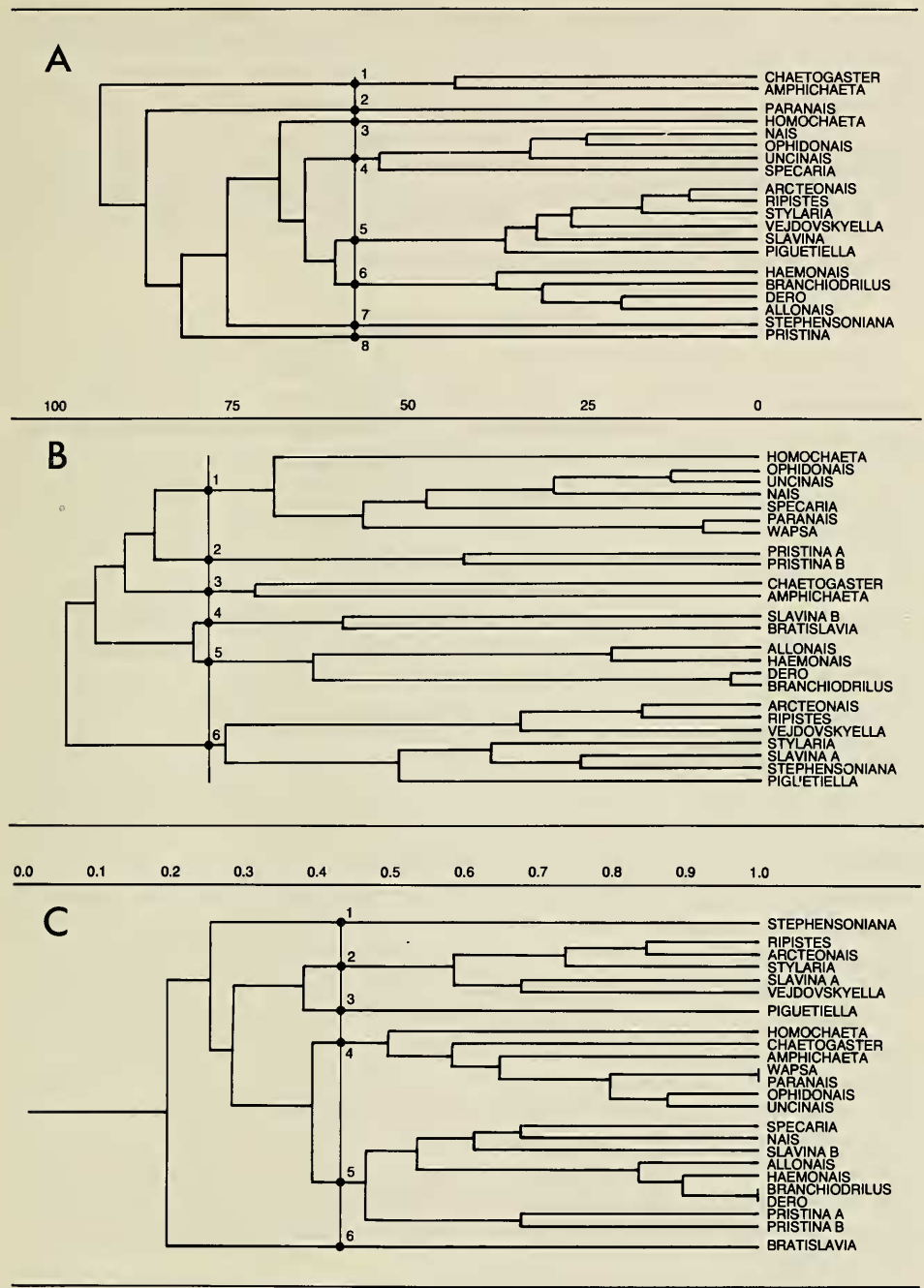


Fig. 1. Dendrograms resulting from re-orientation of an evolutionary tree by Sperber 1948(A), and from cluster analyses of a 15 character by 24 taxa matrix by the methods of Ward (B) and Preston (C). There is no quantitative scale for A as the clusters were created qualitatively.

Remarks.— Full synonymies of these genera plus *Bratislavia* Kosel are discussed by Brinkhurst (1971) and subsequent changes by Harman (1973, 1974, 1982), Harman and McMahan (1975), Harman and Loden (1978), Loden and Harman (1980) and Brinkhurst and Kathman (1983). Other synonymies will undoubtedly be uncovered as recent observations using scanning electron microscopy continue to reveal intraspecific variation in the degree of serration of hair setae, the presence of pectinations in normally bifid setae, and the effects of environmental conditions on setal form. Care should be taken in separating species currently distinguished by such characters (e.g., *P. longidentata* and *P. idrensis*).

Quantitative Analysis

A variety of quantitative methods are being evaluated using a data matrix derived from the characters used to define naidid genera. A 24×24 matrix of characters and taxa is used, with *Pristina* and *Slavina* divided into two taxa each, and the recent genera *Neonais* Sokolskaya and *Rhopalonais* Dzwillo and Grimm excluded by reason of lack of knowledge of the reproductive structures. A condensed data matrix of only 15 characters was created by eliminating those characters thought to be less reliable by virtue of the difficulty experienced in scoring them, or their dependence on other characters. Serrations on the hair setae, for example, may vary in degree of development and their existence depends on the presence of hair setae in the first instance. For the purposes of this discussion only three cluster diagrams will be used (Fig. 1). The first was derived from the evolutionary tree proposed by Sperber (1948). The dendrogram was created by measuring the distances between dichotomies on the evolutionary tree, and so there is no scale of similarity involved (Fig. 1A). The four subfamilies form monophyletic groups, identified as groups 1, 2, 8, and 3-7 respectively. The analysis according to the Ward method (Ward 1963) is illustrated in Fig. 1B, that by the Preston method (small input pair-group cluster, unweighted pair-group mean clustering optimum rotation of dendrogram, Preston's resemblance equation Preston 1962) in Fig. 1C. Both of these were based on the shorter, more reliable data set. The features of these dendrograms referred to here are consistent in all of the analyses performed to date, though other details vary quite considerably.

The points to be emphasized here are that there is no evidence to support the separation of the subfamilies proposed by Sperber, and that, while the two sections of *Pristina* cluster together, they do so at a lower level of similarity than a great many other genera currently regarded as well established. Examples of the latter would be *Dero* Oken with *Branchiodrilus* Mich. (which always pair so closely that a single origin of gills in the family can be postulated) and *Ophidonais* Gervais with *Unicinai* Lev. The similarity of *Paranais* and *Wapsa* Marcus was rendered total when the latter was shown to be a synonym of the former by Brinkhurst and Coates (1984).

These results are obtained with both the Ward and Preston analyses (and others) despite the fact that the first method recognizes all similarities (0-0, 1-1) whereas the latter only recognizes positive matches (1-1) in a Hennigian manner. The data were polarized with respect to a supposed ancestor in the Preston analysis as required by the method.

In a later presentation, the data matrix will be discussed in detail, and the

possible new subfamilial groupings derived from a variety of phenetic and cladistic methodologies will be explored.

Acknowledgments

I am indebted to A. F. Nemec, S. F. Cross, and D. C. Jeffries for statistical analyses and advice, and to R. D. Kathman for reviewing the manuscript. M. Stone typed several drafts of the manuscript.

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Ocean Ecology Laboratory, Institute of Ocean Sciences, P.O. Box 6000, 9860 West Saanich Road, Sidney, British Columbia V8L 4B2, Canada.